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## WHY DO CALIFORNIA TORTOISESHELLS MIGRATE? <sup>1</sup>

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THE CALIFORNIA TORTOISESHELL BUTTERFLY, *Nymphalis californica* Boisduval (Nymphalidae), is well known to entomologists and laymen alike on the Pacific Coast for its mass movements. The biological basis for these movements has always been obscure. After discussing notable outbreaks in the Yosemite region, Garth and Tilden (1963) say: "The explanation seems to be that the California Tortoiseshell is a swarming species which, like the lemming, has cycles of abundance followed by a drastic reduction in the population . . ." But this is obviously no *explanation* at all. Powell (1972) wrote that "the records suggest that this species periodically develops an imbalance with factors in its population equilibrium at isolated sites, followed by mass emigration of adults in various directions. . . . *Nymphalis californica* should not be considered a migratory species except in the broadest sense." This is a more definitive statement, but it also falls short of being an explanation. Mass movements of butterflies, as Klots (1951) observes, have been attributed to "population pressure" and "parasite pressure." Just what do such "explanations" mean?

Let us assume that the word "migration" is applicable to *N. californica* as I intend to show it is. If we ask "Why do California Tortoiseshells migrate?" we are not asking a simple question. Ernst Mayr (1961) pointed out in a classic paper that any "why" question in biology may be answered at several levels. Mayr actually addressed himself to a question about migration: "Why did the warbler on my summer place in New Hampshire start his southward migration on the night of the 25th of August?" Mayr perceived at least four equally legitimate levels of causality:

1) *an ecological cause*. "The warbler, being an insect eater, must migrate, because it would starve to death if it should try to winter in New Hampshire."

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2) a *genetic cause*. "The warbler has acquired a genetic constitution in the course of (its) evolutionary history which induces it to respond appropriately to the proper stimuli from the environment."

3) an *intrinsic physiological cause*. "The warbler . . . responds to the decrease in day length and is ready to migrate as soon as the number of hours of daylight has dropped below a certain level."

4) an *extrinsic physiological cause*. ". . . sudden drop in temperature and associated weather conditions affected the bird, already in a general physiological readiness for migration, so that it actually took off on that particular day."

Mayr groups (3) and (4) as *proximate* causes of migration—the immediate triggering mechanisms. Causes (1) and (2) he calls *ultimate* causes—"causes that have a history and that have been incorporated into the system through many thousands of generations of natural selection." Clearly a physiologist, asked our "why" question, would refer to proximate causes; an evolutionist, to ultimate ones. Equally clearly, cause (1) is the basis for the natural selection which brought (2) into being, and (3) is the phenotypic manifestation of the genetic information in (2), and is brought into action by (4). This method of causal analysis is theoretically applicable to any adaptation; and by its use we may perhaps be spared the travail of endless controversies over the significance of a phenomenon such as hilltopping behavior in butterflies and other insects, or of "territoriality" in anything. Let us now try to analyze levels of causality in the light of what we know of *Nymphalis californica* migrations—which is not much, but is considerably more than many people think we know.

I have been watching Tortoiseshell migrations for the past four years, and unlike most Tortoiseshell watchers, I have been chasing them. When you follow their movements from place to place—not by individual marking, which would truly be a needle-in-the-haystack operation, but by keeping track of where the front of the migration is on consecutive occasions—it becomes clear that, at least at the latitude of Sacramento, Powell is dead wrong: Tortoiseshells do not go in all directions; they have a set seasonal directionality, with a spring-fall reversal. The confusion in many published reports is based at least in part on the "static observer" effect and on local eddies in the migratory flow produced by topography. But California Tortoiseshells go

north and east in May and June and south and west in September and October. The generalized pattern is for dispersal out of the central Coast Ranges in spring—northward in the higher ranges, especially from Colusa County north, eastward from the lower ranges in Napa, Yolo, and Solano Counties, crossing the floor of the Sacramento Valley and going up the Sierra foothills east of Sacramento. Almost simultaneously Tortoiseshells migrate out of the Sierra foothills, heading upslope in a N to NE direction. The two currents generally merge. The pattern is exactly reversed in the fall; again the migrants can be seen crossing the Valley floor, where they never breed (there being no hosts). This pattern, first described in my 1974 paper based on 1972 observations, has been repeated unerringly in successive years; and as I get more sophisticated at Tortoiseshell-watching, I am getting better too at predicting the dates. They are rather variable; for example, the eastward-moving spring front passed through Davis on 26 May 1972, 9 June 1973, 6 June 1974, and 13 June 1975. Based on this small sample, the warmer and drier the spring, the earlier the flight. These migrants are, of course, not the adults which crossed the Valley the autumn before and overwintered (very few Tortoiseshells seem to remain in the lower Coast Ranges through the summer, and the hibernators are mostly or all immigrants from the north or east). They are their offspring. And the return migrants in fall are *their* offspring, or even their grandchildren.

The regularity of this pattern suggests that it is an adaptation, an attribute of the animal which promotes its welfare. Being an evolutionist, I am most interested in the ultimate levels of causality—the basis of natural selection resulting in the acquisition of a genetic program which instructs the animal to migrate in such and such a direction given such and such (proximate causality) conditions.

Why should *Nymphalis californica* leave the lowlands in both the Coast Ranges (which are often only foothills without any mountains) and the Sierras? Of course, it could be heat-intolerant. After all, its host plants, wild lilacs (*Ceanothus* species, Rhamnaceae), are green all summer; presumably it could breed continuously in the lowlands if it "wanted" to. Instead it leaves the foothills, with their *Ceanothus* species, to go breed in the high country and the north, with a different set of *Ceanothus*. It could be heat intolerance, acting directly; but I think not. Being a Pierid specialist, with a dislike for

Nymphalids as experimental animals, I do not want to test the following hypothesis myself. It would make someone a nice Ph.D. thesis, as well as being a good exercise in Mayr-style causal analysis.

In 1970, P. P. Feeny, from Cornell, published a landmark study of the role of host-plant chemistry in insect phenology. Feeny found that the spring feeding season of Winter Moth (*Operophtera brumata* L., Geometridae) larvae coincided with the period of minimal tannin concentration in their food—oak leaves—and that the higher tannin concentrations characteristic of mature, summer oak foliage interfered with nitrogen availability and perhaps leaf palatability to the larvae. Feeny was thus able to develop a causal explanation of spring feeding by Winter Moth larvae as an adaptive response to the seasonal pattern of nutritional “availability” of oak foliage. The insect faunas of high-tannin plants throughout the Northern Hemisphere appear to show this effect. Shapiro (1975) gives a schematic representation for some oak-feeding Lepidoptera in New Jersey, for example. Similar schemata could be prepared easily for Californian faunas on native oaks or on other high-tannin plants, such as *Cercocarpus*—or *Ceanothus*.

I am suggesting that California Tortoiseshells leave the lowlands and go upslope in spring because the lowland *Ceanothus* put on all their new growth in late winter-early spring and become nutritionally unsuitable for breeding by June. The higher one goes, the later the *Ceanothus* commence active growth and hence the later they have young, tender, hypothetically low-tannin foliage available for Tortoiseshell larvae. The seasonality of lowland *Ceanothus* of course reflects the arid-summer climate, so indirectly at least climate may be a “cause” of Tortoiseshell migrations. But, in Mayr’s sense, the ultimate cause—the ecological cause—would be the correlation of geography and availability of *Ceanothus* foliage. In California’s progressively drier Quaternary summer climate, a *Ceanothus* feeder unable to handle tannins has a “choice” between being sedentary and univoltine or migratory and multivoltine; I propose that *N. californica* has evolved along the latter course.

Sometimes the proximate and ultimate causes coincide, in whole or in part. The proximate causes of Tortoiseshell migrations could involve a response to the chemical or textural condition of the plants. They could also be tied to photoperiod, temperature, or some other seasonal indicator—we know not



what. At present, however, there is nothing to suggest that either population density or "parasite pressure" has anything to do with it. Based on my four years of careful observation, I am willing to assert that migration occurs in the directions described with population densities fluctuating by at least two orders of magnitude. If the host-availability hypothesis holds up, this would scarcely be surprising; inedible plants are inedible whether there are a few or a lot of hungry caterpillars.

In recent years major strides have been made in the understanding of insect migration, e.g. the sophisticated studies by Dingle (1968, 1972) and his colleagues on milkweed bugs (Hemiptera, Lygaeidae) in North America. There is no reason why butterflies should be any more difficult to unravel, especially once we realize that explanations at different levels are not mutually exclusive (but, rather, mutually complementary), and that naming a phenomenon ("swarming species," "cycles of abundance") is not the same as explaining it.

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